Divergence of the potential invasion range of emerald ash borer and its host distribution in North America under climate change

Liang Liang · Songlin Fei

Abstract Climate change is likely to induce range divergence of invasive herbivore insects and native host trees given their different response rates to temperature increase. In this study we used the invasion of emerald ash borer (EAB, *Agrilus planipennis* Fairmaire), which is host-specific to ash (*Fraxinus* spp.), to demonstrate the significant implications of this climate change induced insect-host divergence for management of invasive species. The least constrained climatic limits of EAB were derived from its native range in East Asia, then projected to North America under the current and future climate conditions, and finally compared with the assumedly static ash distribution. Results suggest that the divergence between the invasion range of EAB and the distribution of ash in North America is likely to enlarge as climate change proceeds. In this case, many original ash stands could remain intact in the southern range, possibly forming refugia of the host species. The realization of this prediction, however, requires that the spread of EAB be reduced by continued management effort to allow climate change to take effect in time. Our study highlights the important role climate change has in the course of biological invasion and herbivore-host dynamics, which provides key information for continental scale pest risk prediction and strategic planning.

1 Introduction

As evidenced by both empirical and theoretical studies, climate change results in species range shift (Chen et al. 2011; Kelly and Goulden 2008). However, a key challenge remains regarding how climate change will interact with other stressors, such as invasive species, to impact biodiversity (Rosenzweig et al. 2007). In particular, insect herbivores are expected to have more

L. Liang (✉)
Department of Geography, University of Kentucky, 817 Patterson Office Tower, Lexington, KY 40506, USA
e-mail: liang.liang@uky.edu

S. Fei
Department of Forestry and Natural Resources, Purdue University, 221E Pfendler Bldg., 715 West State St., West Lafayette, IN 47907, USA
e-mail: sfei@purdue.edu

rapid latitudinal or elevational shifts compared to their host species (Chen et al. 2011; Hodkinson and Bird 1998), which has significant implications for conserving native plants affected by invasive insects.

The emerald ash borer (EAB, *Agrilus planipennis* Fairmaire), native to Asia, is an invasive wood-boring beetle that has caused widespread ash (*Fraxinus* spp.) mortality in North America (Kovacs et al. 2010). EAB was first reported killing millions of ash trees in southeast Michigan, U.S. and neighboring Ontario, Canada in 2002 (Haack et al. 2002). It was speculated that EAB may have been inadvertently imported into ports of Detroit and Windsor a decade before its initial discovery, probably through wood packing materials used for international cargo shipping (Cappaert et al. 2005; Poland and McCullough 2006). The natural expansion of EAB only occurs at a local scale and its long-distance spread is facilitated by moving and transporting infested ash trees/nursery stocks, logs, or firewood.

The primary regulatory strategy is to create quarantine zones by state and federal agencies to limit the spread of potentially infested materials. Federal quarantines were put into effect by the Canadian Food Inspection Agency (CFIA) in 2002 and by the U.S. Department of Agriculture (USDA) Animal and Plant Health Inspection Service (APHIS) in 2003. Despite these actions, and perhaps also due to improved detection ability, EAB has since been found in 20 U.S. states and two Canadian provinces in Canada (http://www.aphis.usda.gov). Moreover, profound ecological impacts of ash tree loss on forest health have begun to emerge (Gandhi and Herms 2010; Hausman et al. 2010).

Rigorous research has been done to develop effective control techniques since the discovery of EAB's invasion (Cappaert et al. 2005; San Souci et al. 2009). Common procedures include detecting, removing and quarantining infested ash stands, restricting ash wood transportation, attracting and concentrating EAB for destruction, harvesting ash trees to reduce food source, applying insecticides, and biological control using parasitoids (USDA–APHIS 2013; www.slameab.info). These practices are critical for reducing EAB population growth and expansion, and should remain a focus of study. However, in the case that EAB becomes established in broader regions of the continent (Kovacs et al. 2010), it is useful to additionally inquire the possible existence of natural limits to its spread.

The fundamental limit on EAB range is the distribution of ash trees, given the insect's high host specificity (Anulewicz et al. 2008; Rebek et al. 2008). However, to conserve ash resources, it is important to further investigate other constraints that could limit EAB's distribution. Indeed, in its native East Asian range, EAB is only found within a fraction (less than 1/2) of the host plant distribution, leaving a large extent of ash trees unexploited by the herbivore in southern China (Wei et al. 2004; Fig. 1), suggesting that other environmental factors may further limit its geographic range. It is known that the distribution of poikilothermic (cold-blooded) insects is regulated by temperature regimes (Gillott 1995). EAB, in particular, requires an overwintering stage for larvae development and a subsequent spring-to-summer period for adult activities, suggesting that proper temperature range and seasonality are necessary for EAB's life cycle fulfillment (Jonathan Lelito, USDA-APHIS, personal correspondence). Additionally, biotic agents such as pathogens, parasitoids, and predators may impose stresses on the insects, but primarily at the local scale (Duan et al. 2010; Lindell et al. 2008).

To support EAB management, existing studies have focused on short-term and regional scale patterns in affected regions (Muirhead et al. 2006; Prasad et al. 2010). Little attention has been given to examining the long-term and continental scale expansion risks of the insect. Recent research employed species distribution models to investigate the potential distribution of EAB in North America under the current climate conditions (Sobek-Swant et al. 2012), but
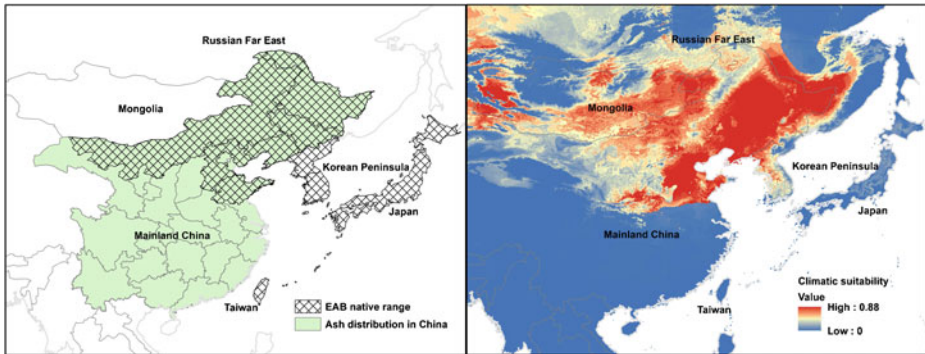
Fig. 1 Map (*left*) of the native emerald ash borer (EAB, *Agrilus planipennis* Fairmaire) range in East Asia (excluding Mongolia and Russian Far East) and ash species distribution in China according to Wei et al. (2004). Predicted climatic suitability (0-1 ratio) for EAB in East Asia (right)

has not considered the impact of climate change. Therefore, in this study we predicted the maximum potential range of EAB invasion and its decoupling with its host tree distribution as driven by the changing climate in North America, based on the assumption that EAB has far more rapid movement in response to warming than its host species.

2 Methods

2.1 Native range and climate of EAB

EAB's native range provides the basis for deriving climatic boundaries for the species. Historical records and exploratory surveys indicated that EAB's native distribution is centered in northeast China and extends to neighboring Mongolia, Russian Far East, Korean Peninsula, Japan, and an outlying distribution in Taiwan (Fig. 1; Liu et al. 2003; Wei et al. 2004). The distribution generally overlaps with the humid continental climate with cold winters and warm to hot summers, and a northern portion of the humid subtropical climate (Rohli and Vega 2008). Wei et al. (2004) produced a relatively detailed EAB distribution map at the county level in China, occupying the northeast and northern central plains of the country. For neighboring regions, however, little information is available for delineating exact EAB range except for national boundaries. In consideration of this uncertainty, we adopted a broad approximation of EAB's native range in order to capture the maximum climatic limits of the insect. This estimated native range covered the entire Northeast China (including all provinces with documented EAB presence, and the western portion of Inner Mongolia) as described in Wei et al. (2004) and included the entire Korean Peninsula, Japan, and the outlying distribution in Taiwan. Russian Far East and Mongolia were not included because their extensive national territories may lead to significant overestimation in the northern range. This native range estimation covered a much larger southern range than the point samples in part of Northeast China, Korean Peninsula, and Japan as used in a previous study (Sobek-Swant et al. 2012), except that two points in the northern range (used in the same study) located near but beyond Northeast China were not included. Allowing a broad and less constrained southern range would help to ensure that the predicted geographic divergence of insect-host distributions in the south under climate change is not resulted from an underestimation of the native range if determined by climate.

2.2 Ash distribution and climate change scenarios

Digital range maps for native ash species in North America (Little 1971) are available from the USGS (http://esp.cr.usgs.gov/data/atlas/little/). In this study, we focused on the following major ash species: green ash (*F. pennsylvanica*), white ash (*F. americana*), blue ash (*F. quadrangulata*), and black ash (*F. nigra*). The combined range (Fig. 2) of these four species
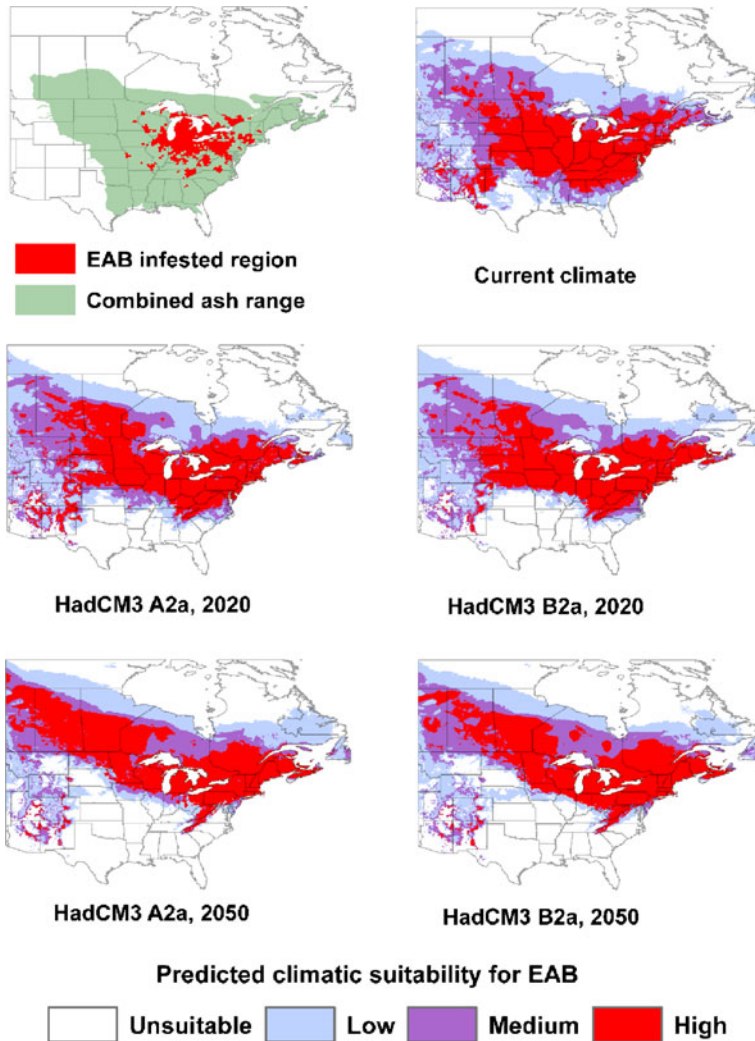

Fig. 2 Emerald ash borer (EAB, *Agrilus planipennis* Fairmaire) infested areas as of September 5, 2013 (USDA-APHIS) and the distribution of major ash (*Fraxinus*) species (*top left*); current EAB climatic suitability prediction by relative risk rankings based on climate data 1950–2000 in North America (*top right*); and projected climatic suitability predictions for EAB in North America according to selected IPCC scenarios (HadCM3 A2a and B2a) for 2020 and 2050. Host plant range is a combination of four primary ash species: green ash (*F. pennsylvanica*), white ash (*F. americana*), black ash (*F. nigra*), and blue ash (*F. quadrangulata*) according to Little (1971). The respective ranges of each ash species relative to the current EAB infested region are shown in Appendix Fig. 1. The underlying background provides state and province boundaries in the U.S. and Canada

covers a large part of eastern North America. A comparison between Little (1971)'s estimates (portions within the U.S.) and more recent U.S. Forest Service Forest Inventory Analysis (FIA) survey (Map Atlas Web Tool, available for white ash and green ash only) showed minimal differences. This historical estimate of ash species range was used for comparing with potential future expansion of EAB based on the assumption that the distribution change of the host tree species will be minimal as induced by climate change in the near term (e.g., towards the midpoint of this century). This assumption is first supported by the fact that insect herbivores have higher sensitivity to a changing climate, and their range shifts tend to take place far more rapidly than observable alterations of the host plant distribution (Chen et al. 2011; Hodkinson and Bird 1998). In addition, according to specific model predictions, ash species range shifts could be minimal and the southern distribution of ash species will continue to persist along the Gulf of Mexico coast under future climate conditions (Iverson and Prasad 1998).

Climate data used were from the WorldClim dataset which provides interpolated monthly climate surfaces covering global land regions (Hijmans et al. 2005; http://www.worldclim.org/). Data describing current conditions were based on averaged monthly temperatures from 1950 to 2000. Future predictions were derived according to emission scenarios as prescribed in the Third Assessment Report of Intergovernmental Panel on Climate Change (IPCC 2001). A moderate B2a scenario and an extreme A2a scenario were selected using projection outputs from the Hadley Centre Coupled Model, version 3 (HadCM3), for 2020 and 2050 respectively. We utilized data layers at a spatial resolution of 5 arc-minutes, for both East Asia and North America. In addition, we performed an estimate of EAB's southward spread rate over the past 5 years (2008–2013) based on historical ranges. This time period was chosen because the ascertained range expansion in earlier years (2002–2007) may be more affected by increased detection capabilities. At the current rate for long distance "jump" dispersal (~ 80 km/year) the insect may take as less as 7 years to reach the southern edge of ash range.

2.3 Bioclimatic modeling and EAB environmental constraints

Modeling the distribution of invasive species is based on the environmental conservatism that assumes that a species can only survive in introduced environments with conditions that match those of its native range (Peterson 2003; Wiens and Graham 2005). Hence, predicting EAB's potential invasion range can be achieved with species distribution modeling driven by climatic constraints specified by its native range. We employed the maximum entropy approach (Maxent) to predicting EAB distribution (Elith et al. 2011; Phillips and Dudík 2008). The theory behind the Maxent modeling technique defines an optimum estimate of probability distribution of a species over an area as one that yields maximum entropy (most uniform), on the condition that all known environmental requirements are met. Maxent is a widely used tool for ecological niche and climate envelope modeling and is useful for generating predictions of species distribution under climate change (Hijmans and Graham 2006; Phillips 2008).

There is little species-specific information available in the literature concerning EAB's environmental physiology. Given that EAB is a poikilothermic insect and is found in moist climates where forest growth is supported, temperature likely plays a major role in limiting the insect's distribution (Gillott 1995; Dixon et al. 2009). Indeed, EAB's life cycle fulfillment is dependent on a temperate climate with distinct warm and cold seasons (Jonathan Lelito, USDA-APHIS, personal correspondence). First, sufficient heat energy is a prerequisite to allow completing an annual or a biannual (in colder conditions) reproduction cycle from EAB egg to adult. Warm temperature with sunshine is necessary during the adult flight for successful mating, oviposition, and early larvae development. In addition, a cold winter season is required for diapause initiation and break. EAB larvae that do not experience this cool period

will not initiate adult development, or will do so sporadically and produce stunted adults. Existing literature does additionally suggest that EAB larvae survival is limited by low temperatures during the overwintering stage (Venette and Abrahamson 2010; Vermunt et al. 2012) and the insect has facultative diapause (Bauer et al. 2003) which is tied to seasonal weather change. Therefore, both the south and north ranges of EAB are highly sensitive to annual temperature regimes (Bale and Hayward 2010). Besides, the brief span of EAB adult activities (approximately 3 weeks) is concentrated around the month of June (Lyons and Jones 2005; Wang et al. 2010), implying that the minimum temperature of June may be an additional limiting factor. Therefore, according to these implications of EAB physioecology, we selected the following variables from the WorldClim dataset to characterize the temperature regimes that potentially limit EAB's distribution: minimum temperature of coldest month (low extreme), maximum temperature of warmest month (high extreme), annual temperature range (seasonality), and minimum temperature of June.

2.4 EAB climate suitability prediction

In deriving the climatic limits of EAB's native distribution, we sampled the native range of EAB in East Asia using an evenly spaced 15 arc-minutes grid, yielding 5,107 points. The data points were partitioned into training and testing datasets. According to a heuristic rule (Fielding and Bell 1997; Huberty 1994), 37 % of data points were reserved for testing, while the remaining were used to construct the models. A relatively large 50,000 points background sampling limit was used to ensure that the climatic characteristics of EAB distribution can be extracted from the overall area of interest (i.e., East Asia). The models first generated predictions for EAB's native range, and then produced predictions under respectively the current and future climate conditions over eastern North America. Each model was executed in 10 replicate runs with data points randomly repartitioned each time according to the same specified ratio. Outputs of 10 replicate runs were averaged to generate a consensus climatic suitability prediction for each case. The outputs of Maxent models were in the format of raster data with every pixel attributed a presence probability ratio (0-1), indicating the climatic suitability in the context of this study. Given that the outputs were threshold-independent continuous variables, model performance evaluation was based on receiver operating characteristic (ROC) analysis (Zweig and Campbell 1993). The area under ROC curve (AUC) was used as an index to assess whether a model prediction is better than random and to provide an overall accuracy estimate (Fielding and Bell 1997).

To better interpret the continuous climatic suitability spectrum within an invasion risk ranking framework, a multi-threshold approach was used to further delineate climatic suitability classes based on the sum of sensitivity and specificity index (Fei et al. 2012; Supplementary Note). The multi-threshold approach allowed stratifying continuous prediction results into climatic suitability classes (i.e., unsuitable, low suitability, medium suitability, and high suitability) that are convenient for risk level assessment. The predicted climatic suitability zones were then compared with the native ash range to evaluate their overlaps and divergences over time. Environmental variables used were investigated with information provided in Maxent model outputs. In particular, relative importance of a variable was evaluated using estimates of percentage model contribution. In addition, diagnostic models using every variable separately were tested, yielding response curves showing the variation of suitability predictions with the change of each environmental factor, respectively. The ranges of climate conditions favorable to EAB were delineated by extracting the lower limit and upper limit of each variable from their response curves using the threshold for medium and above suitability as a cutoff point.

3 Results

3.1 Climatic suitability models

According to calculated AUC values (0.81-0.83), all Maxent models performed with good accuracy (AUC>0.8) and captured patterns far from random (AUC>0.5) for every replicate run and under the respective climatic conditions (Appendix Table 1). The predicted climatic suitability gradients closely matched the boundaries of EAB's native range in East Asia (Fig. 1). Eastern Mongolia and Russian Far East, which were known to have EAB presence but excluded from model inputs due to the unknown boundaries within these two countries, were predicted to have higher climatic suitability. A portion of the North China Plain not included in the EAB range was also predicted with high climatic suitability. Taiwan and Japan, which were known to have reported EAB presence, were predicted to have lower climatic suitability, except for the mountain ridges of Japan where the climate appeared more suitable for EAB than low lying areas. Overall, the model appears to have captured the least constricted climate limits of the insect covering a broader region containing most of its known native range.

All environmental variables played important roles in the models as indicated by their percentage contribution estimates (Appendix Table 2). The minimum temperature of June appears to have contributed the most (> 50 %) to the model, while annual temperature range, annual maximum temperature, and annual minimum temperature contributed 20.5 %, 14.5 % and 13 % to the model, respectively. Predicted climatic suitability is responsive to specific ranges of environmental variables (Appendix Fig. 1). The cold temperature limit for EAB climatic suitability is approximately -38°C, comparable to experimental study results according to Venette and Abrahamson (2010). The high temperature limit is around 33°C. A minimum 27.5°C annual temperature range appears to be necessary as indicted by the value defined at the southern limit (excluding Taiwan which has an outlying minimum temperature range of 14.5°C). Finally, minimum June temperatures that supported favorable climate for EAB lie between 7°C and 19°C.

3.2 Predicted divergence of EAB and ash distributions

The predicted suitable climate zones in North America under the current climate match ash distribution in both spatial patterns and extent (Fig. 2). The high suitability zone covers majority of the infested region as well as adjacent states and provinces. The low suitability zone extends all the way to the Gulf of Mexico coast, closely matching the combined ash range. The overall suitable climate zones (from low to high suitability) for EAB covers more than 94 % of the range for each ash species respectively (Table 1; Appendix Fig. 2). In particular, the predicted suitable climate zones cover the blue ash range completely, surpassing the northern ranges of white ash, green ash and black ash. Only small fractions (<6 %) of the white ash and green ash distribution are predicted with unsuitable climate.

The suitable climatic zones will shift markedly northward under both climate change scenarios (Fig. 2), leading to increased divergence between the distributions of the insect and its host (Table 1). According to this prediction, the current EAB infested area in the Great Lakes region/U.S.-Canada border will remain a center with highly suitable climate for the insect in the future. Towards 2020, however, noticeable areal decreases in insect-host overlap will occur for white ash, green ash and blue ash. In 2020, 80 % of the combined ash range will remain within the generally suitable climate for EAB, leaving about 14 % of ash range in the south (mainly comprised of white ash and green ash) beyond the reach of the insect. From 2020 to 2050, a more significant decrease of pest-host range overlap up to 20 % is predicted to

Table 1 Spatial overlap (in percentage) of current and future emerald ash borer (EAB, *Agrilus planipennis* Fairmaire) climatic suitability zones with the range of primary ash (*Fraxinus*) species in North America: green ash (*F. pennsylvanica*), white ash (*F. americana*), black ash (*F. nigra*), and blue ash (*F. quadrangulata*)

	Climatic suitability	1950–2000	2020 (A2a)	2020 (B2a)	2050 (A2a)	2050 (B2a)
White Ash	Low	9.30	9.13	8.41	8.55	7.88
	Medium	18.01	11.14	6.29	4.65	2.83
	High	67.98	56.09	56.08	38.81	42.96
	Total	95.29	76.35	70.77	52.01	53.67
Green Ash	Low	10.24	8.51	6.77	9.17	8.80
	Medium	28.76	18.50	16.04	8.09	8.83
	High	55.15	52.03	52.16	38.80	39.59
	Total	94.15	79.04	74.97	56.06	57.22
Blue Ash	Low	0.27	14.91	17.46	21.02	19.84
	Medium	0.39	21.56	5.11	14.34	1.03
	High	99.34	61.35	59.75	7.54	24.63
	Total	100.00	97.81	82.32	42.90	45.51
Black Ash	Low	15.06	7.37	5.25	1.97	1.97
	Medium	30.40	16.57	15.30	15.59	15.59
	High	52.77	75.34	79.07	81.99	81.99
	Total	98.23	99.28	99.61	99.55	99.55
All Species	Low	13.37	9.90	7.83	8.35	8.09
	Medium	29.73	19.99	18.02	10.57	10.83
	High	50.99	50.62	51.05	40.83	41.90
	Total	94.09	80.51	76.90	59.75	60.82

occur. Most of this change will be contributed by the northward shift of suitability zones away from the ranges of white ash, green ash and blue ash. Black ash, which is distributed at higher latitudes than other species, is predicted to be constantly associated with suitable climates and with increased high climate suitability coverage. While a large southern portion of the ash range comprised of white ash, green ash and blue ash is projected to be gradually left outside of the suitable climate zones for EAB as the climate changes. By 2050, only about 60 % of the entire historical ash range, mostly the middle and northern portions, covering the entire black ash range, will still remain in the generally suitable climate for EAB.

4 Discussion and conclusions

Our models appear to have captured the main climatic constraints on EAB distribution based on the general agreement of predicted and observed patterns of EAB distribution in both East Asia and North America. The relatively low climatic suitability for Taiwan and Japan is likely due to that EAB in these regions are limited to the colder mountainous locations where climate is similar to that of its continental range. In North America, existing distribution of EAB generally agreed with the high climate suitability zones predicted. Therefore, the Great Lakes region appears to have provided a favorable climate for EAB to initially establish, develop, complete growth cycles over years, and expand its current range to neighboring regions. Our prediction under current climate confirmed a general view that EAB's impact on ash trees is

likely to be extensive, potentially affecting the majority of, if not all, native ash trees/forests on the continent.

Projected future EAB climatic suitability in North America implies that climate change will tend to push EAB expansion north, limited only by the northern boundaries of the host plant distribution. Hence, the consequence with this potential invasion course will be to save a considerable amount of original ash stands in the southern U.S., on the condition that EAB spread will be slowed by effective control measures, so decadal and multi-decadal climate changes will take effect in time. On the other hand, it appears that there will be a long-lasting risk to ash at its northern range. In particular, EAB invasion along and north of the U.S.-Canada border, affecting most part of black ash range and the northeast white ash range where a greater abundance of the species is found, may be exacerbated by climatic warming. Furthermore, the spread rate of EAB might be faster in areas with ash sparsely distributed given that adult beetles have to fly farther to find hosts, but large gaps between ash stands may also frustrate EAB's natural dispersal. At the continental scale, white ash generally has lower abundance towards south, while green ash is more evenly distributed (FIA Map Atlas Web Tool). This implies that the invasion dynamic of EAB, the locations of potential host refugia, and the needed regulatory and control measures may be closely affected by the within range density variation of ash species (MacFarlane and Meyer 2005).

Climate change could contribute to limiting the southward invasion of EAB, given the insect's strong reliance on suitable climate conditions. Besides the low temperature tolerance which controls EAB's northern range, the life cycle fulfillment of the insect particularly requires a strong seasonality with cold and sufficiently long winter season (Jonathan Lelito, USDA-APHIS, personal correspondence), limiting the insect's ability to survive in warmer yet less seasonal climates. In addition, the life history of herbivore insects is coupled with the growth rate of host plants; and the phenological asynchrony between the insect and its host due to differential development rates may be a further limiting factor on the insect's distribution range (MacLean Jr 1983; Bale et al. 2002). Precise environmental biology of EAB and its phenological synchrony with host trees still require more investigation. But the impact of climate limits and climate change on EAB distribution and the insect-host relationship is unequivocal.

Our predictions on the amount of geographic divergence between distributions of EAB and native ash under climate change may be overestimated if the host species experiences notable northward range shift in the coming decades, which however is unlikely to match the magnitude of range shift of the insect itself (Hodkinson and Bird 1998; Iverson et al. 2008). Actually, plant response to climatic change is firstly via phenological timing shift which precedes more profound changes in spatial distribution (Cleland et al. 2007; Chuine 2010), likely making plant species range shift a significantly slower process which lags behind more mobile organisms such as insects. Besides, the amount of spatial divergence may be less if the invaded EAB could extend its environmental adaptability, allowing it to go beyond its native climatic limits, given the insect's high fecundity in North America due to the absence of natural enemies and abundance of preferred host source. However, the possibility of climatic niche shift of invasive species in general is nonetheless very low and environmental conservatism still holds for the majority of biota (Strubbe et al. 2013; Petitpierre et al. 2012). Our adopting a broad and least constrained native range may partly account for EAB's potential stretch from its predicted invasion range.

The omission of Russia Far East and Mongolia in native range estimates did not affect evaluating the insect-host distributions, given that the entire northern range of ash is constantly predicted with suitable climate for EAB. This may affect the determined lower temperature limits and lead to southward shift of predicted climate suitability zones and therefore an underestimate of the divergence. However this discrepancy is likely small, given that the native

range model prediction covered part of those omitted regions. In addition, EAB primarily devastates introduced North American ash in its native range, and causes mortality only to stressed native Asian ash trees (Wei et al. 2004). This suggests that the coevolved host resistance limits EAB's population, and might have led to an underestimation of its native range due to detection difficulties. Given that the predicted high climate suitability covered a broader region beyond the known EAB distribution in mainland China, this uncertainty may also be partly reduced. Furthermore, incorporating growing degree day estimates based on daily temperature data is likely to increase the accuracy of EAB distribution modeling. Future work may include performing more precise modeling using daily climate change projection data. Overall, these known limitations are not likely to change the general conclusion that climate change facilitates a potential range mismatch between the herbivore insect and its host, in turn allowing refugia of the host trees to exist naturally and without purposeful human intervention.

Nonetheless, persistent endeavors in pest control and supporting research are necessary, given that EAB invasion is likely to affect 80 % of the ash species range in North America towards 2020 if its spread is not slowed. The degree that climate change can save the native ash species is dependent on how effective the EAB's dispersal is restrained and the rate of spread is reduced over time. Only with a rigorous effort in management with effective containment and control strategies, considerable amount of ash trees (primarily white ash and green ash) in the southern part of the U.S. may be preserved from ultimate EAB infestation. Given that blue ash is less preferred by EAB than white ash and green ash (Pureswaran and Poland 2009), the relatively small range of blue ash that is currently covered by suitable climate may also be partly preserved as suitable climates gradually shift north. Again, we note that ash in more northern portions of its range along and north of the U.S.-Canada border, especially the entire range of black ash, will likely be more at risk under climate change. The broader implication of this study is that better incorporation of climate change in invasive species risk prediction is important for strategic management efforts for conserving affected natural resources.

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